THE ECOLOGY OF CLIFF-TOP HEATHLANDS AT PORT CAMPBELL, VICTORIA

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Ashton, D. H., Williams, R. J. & Mc Donald, M. 2002:09:30. The ecology of cliff top heathlands at Port Campbell, Victoria. *Proceedings of the Royal Sociiety of Victoria* 114(1): 22-41. ISSN 0035-9211.

Vegetation on the uplifted coastal plain at Port Campbell is zoned parallel to the coast and is strongly influenced by the salt-laden winds from the southern ocean. On the most exposed cliff edges the lateritic sandy clays have been stripped off and open halophytic communities occur on the pitted limestone surface. For 200-400 m the vegetation is ground- water heath, the floristic composition of which changes from that dominated by *Leucopogon parviflorus-Poa poiformis* near the cliffs to that dominated by *Leptospermum scoparium- Gahnia trifida* with increasing distance inland. It is eventually replaced by low woodland and dry sclerophyll forest of *E. ovata, E. obliqua* and *Allocasuarina verticillata* . Clones of the latter species form emergent clumps on the heath where they regenerate to seaward by root suckering. Fruiting is very rare, due probably to damage of emergent feathery stigmas by salt aerosols. The occasional presence of halophytes in local microhabitats in the heathland may indicate an accumulation of cyclic salt in certain seasons. Close to the cliff edges duplex podzolic soil is overlain by a deposit of well-drained calcareous marl, which appears to have been blown up from the limestone cliff faces. The extent of this deposit is often indicated by severe chlorosis of a calcifuge shrub dominant, *Leptospermum scoparium*. In addition, the pH and exchangeable Ca^{++} content of the top soil decreases with distance inland from the cliffs suggesting a drift of fine loessic material. Most of the species on the heath regenerate vegetatively after fire, with the notable exception of *Leptospermum scoparium* which here is an obligate seeder. Since species richness of the heathland declines markedly with age, any management of biodiversity conservation using fire frequency needs to take into account the life-form and life history attributes of the major species.

Key words: Ecology, cliff-tops, heathlands, salt-spray, lime-chlorosis.

GENERAL ENVIRONMENT AND VEGETATION

PORT CAMPBELL National Park occupies a narrow strip 27 km long on the SW Victorian coast between Peterborough and Princetown (Fig.1). The Park is famous for its spectacular cliffs and rugged coasts, and is one of Victoria's most popular tourist destinations. Although its average width is only 0.7 km, it contains a rich flora of 641 species, of which 20% are exotic (Grant 1987). Much of the vegetation is heathland, which occurs in a broad band parallel to the cliff tops. Coastal heath is a common vegetation type in Victoria (Barson & Calder 1978), but cliff-top heaths are unusual. Coastal vegetation is also usually strongly zonal, in response to the influence of salt and wind. The survey of the Park by Grant (1987) described the broad vegetation types of the Park, but there have been no detailed studies of the ecology of the heathlands apart from that of McDonald (1989). The aim of this paper, therefore, is to describe the composition and structure of the heathlands, especially the zonation from the cliff-tops inland, along a stretch of the coast in the central section of the Park. We explore the distribution of plant communities in relation to soil types, saline aerosols, historical factors and vegetation dynamics. Species nomenclature is standardised on Walsh & Entwistle 1994, 1996 and 1999.

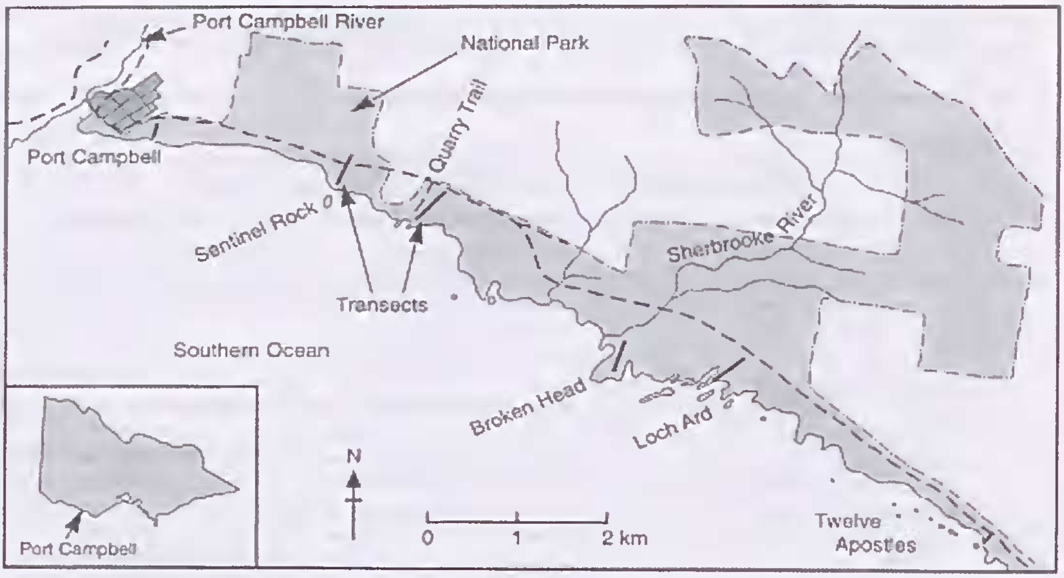


Fig. 1. Location map of the study sites at Port Campbell.

Fig. 2. General view of coast, east of Port Campbell

Physiography, Geology and Land Use

The Park occupies the seaward edge of an uplifted plain which terminates in high, spectacular cliffs of calcilutite (Port Campbell Limestone, Fig. 2) which, although relatively soft, stands in vertical cliffs and may be case-hardened by superficial carbonate precipitation (E.C.F. Bird, personal communication). Rock stacks and blowholes indicate the extent of the active marine erosion along this high energy coast (Bird 1976, 1993). The water table of the area seeps out of the cliffs about 40 m below the surface resulting in limestone shawls and malformed stalactites.

The hinterland is flat or gently undulating plain drained in this area by the two main streams, Port Campbell Creek and Sherbrooke River. Intermittent streams may reach the coast as hanging valleys. The land surface may either slope gently towards or away from the cliffs depending on the drainage systems present. The thick, fossiliferous marine Miocene limestones that underlie the whole region, have been uplifted 40-50 m and and exposed in the cliff faces, the cliff tops and inland along the deeper valleys. Most of the plain is covered with a 2-5 m veneer of non-fossiliferous Pliocene Hesse Clay, consisting of clays, sandy clays and current-bedded fluviatile sands (Gill 1965; Fig. 3).

In some places on the plain small lightly vegetated clay pans occur in the heath which may indicate an earlier dry period of soil deflation. The small tongues of Holocene sand which tend to infill surface irregularities in heathland at Loch Ard and Two Mile Bay, may also be a result of the same processes or may have been derived from beach sands further upwind to the west.

In general, the land surface has been stable since uplift and has revealed an important source of mid-Holocene extra-terrestrial australites (Gill 1965).

Prior to the gazetting of the National Park in 1964 the area was used for rough grazing by nearby farmers. Undoubtedly it was burnt many times both in pre and post European times. A small fire which occurred along the Quarry Trail in 1987 has provided valuable insights into the regeneration of heathlands in this area. However, the detailed fire history of the Park is unknown.

Climate

The climate is typically temperate and maritime with warm summers and cool winters and a general absence of severe frosts. The mean annual rainfall is about 908 mm with a winter maximum. Regional winds vary from predominantly NW in winter to SW in summer although in terms of strong–squally winds this generalization is reversed. Coastal sea breezes from the S-SE are an important component of the summer climate.

Soil

The soils of the area are closely correlated with parent material, topography and the age of the land surface. The predominant soil is a yellow to lateritic podzolic type (Stace et. al. 1968) with a humus-rich sand to sandy loam top soil 15-30 cm deep, above a sandy clay subsoil. Because of the sharp textural change at the A/B horizon boundary the soil type is clearly duplex (Northcote 1965). Buckshot gravel is com-

Fig. 3. Miocene limestone cliffs with an unconformable overburden of younger Pliocene sediments. The water table issues from the lower one third of the cliff face.

Fig. 4. Karst in stripped edges, Loch Ard area.

mon at this boundary and indicative of intermittent waterlogging (Leeper & Uren 1993). Nevertheless texture is variable, and is influenced locally by that of the parent material. In some places where sands predominate, subsoils are low in clay and show induration by coffee rock. In exposures at the cliff faces the deeper layers of sandy clays (2-3 m) are ferrugenized and show conspicuous red, yellow and white mottle. This material may be indurated with calcareous material along cracks for 1-2 m above the limestone disconformity.

Features of the cliff edge environment

On many exposed headlands, stripped cliff top edges (Baker 1958) may be 1-30 m wide and show local rugged erosional surfaces pitted with depressions and solution holes (Fig 4). In stormy weather in May 1987, waves were observed to break onto the cliffs and splash over onto one of the stripped zones. Backwash from such waves as well as run-off from heavy rains have contributed to the severe erosion of this zone.

In places along the near-vertical cliff edges, (such as opposite Sentinel Rock and at Quarry Trail), that are subjected to the full force of onshore winds, a 'berm-like' deposit of edging of undifferentiated yellowish brown marl up to 0.5 m deep resting on what appears to be a palaeosol on the Tertiary lateritized sandy clays (Fig.5). The marl is exposed at the top of cliff faces, thins out rapidly inland and cannot be distinguished after 100-150 m (Fig. 6). Occasional

Fig. 5. The upper section of the cliff near Quarry Trail, showing well structured Holocene marl deposit (1) above old soil profile (2) developed on lateritized Hesse Clay (3).

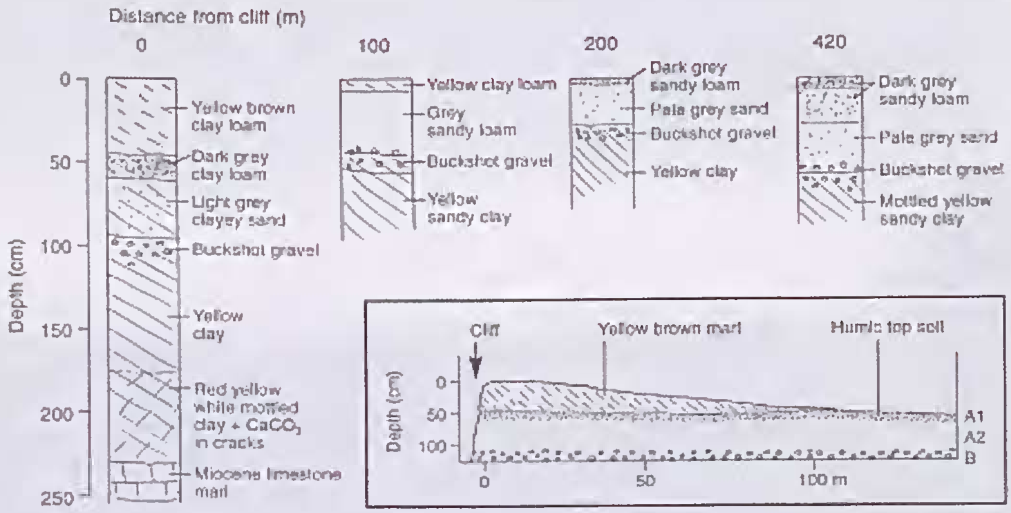


Fig. 6. The variation of soil profiles across the clifftop heathland and a schematic representation of the clifftop marl sediments opposite Sentinel Rock (inset).

Fig. 7. Miocene fan shells from grass tussocks and shrubs at the cliff edge, Sentinel Rock.The largest specimen is *Hinnites* sp and the remainder, *Serripectin* sp

Miocene fossil fan shells (*Hinnites* sp and *Serripecten* sp) and shell fragments (Fig. 7) have been found on the soil surface or amongst grass tussocks at the cliff edge opposite Sentinel Rock. Marl has also collected in bark furrows and branch angles of shrubs of *Calocephalus* and *Leucopogon* in these sites. There seems little doubt that certain of the more aerodynamic fossils (1-5 cm in diameter and weighing 0.2-5.6 g) have been blasted out of soft limestone of the cliff face by squally on-shore winds and deposited on the cliff top. The coarser material (consisting of clay 30%, silt 14%, fine sand 41% and coarse sand 15%) has been deposited at the cliff edge whilst finer material is likely to have been blown inland over the heath in a somewhat analogous manner to loess or parna.

Vegetation

Vegetation is zoned parallel to the coast (Fig. 8). A broad scale survey of the plant communities of Port Campbell National Park by Grant (1987) emphasized the zonation from cliff-top tussock grassland and cushion heath (*Calocephalus brownii*) to different kinds of wet heath and to low, dry sclerophyll forest of *Eucalyptus obliqua* and *E.ovata* in the hinterland. Importantly, as suggested by Grant (1987), the wet, sedge-rich heathlands could be divided generally into

Fig. 8. General view of the grass and heath zonation, Sentinel Rock.

seaward communities characterised by *Leptospermum scoparium*, *Gahnia trifida* and *Baumea juncea* and landward communities characterised by *Leptospermum continentale*, and *Xanthorrhoea australis*. Occasional low bushes of eucalypts (*E. obliqua*, *E. ovata*) may merge with the general heath stratum 200-250 m from the cliffs, but further back these species become emergent with streamlined profiles. Throughout the heath zone conspicuous, widely scattered clumps of *Allocasuarina verticillata* emerge above the associated shrubs to heights of 6-9 m. Continuous low dry sclerophyll forest 5-8 m high, commences about 500 m inland beyond a broad ecotonal mosaic.

DETAILED ECOLOGICAL STUDIES

Methods

Detailed ecological studies were undertaken along a 12 km stretch of the coast, from Port Campbell to the Twelve Apostles (Fig. 1). We examined community structure and composition, soil properties, and plant-environment interactions. The major approach was to document environmental and vegetational changes along six transects up to 420 m long, laid out orthogonal to the coast.

Local climate. Thermohygrographs were set up one metre above ground at intervals along a transect near Sentinel Rock in late February-early March 1987-88. At the same time numerous salt traps, consisting of a tube of fine gauze 2 cm in diameter and 30 cm high, were set up at frequent intervals. After four days the traps were rinsed with distilled water and Cl^- concentration determined with an electrolysis chloride meter. Foliage of selected species at these locations was also collected, rinsed with distilled water, made up to standard volume and the concentration of Cl^- determined and expressed in terms of unit leaf area. Leaf anatomy of various species was also investigated in exposed and sheltered sites.

In a study of the root suckering regeneration of *Allocasuarina verticillata*, soil temperatures were measured by burying max-min thermometers at a depth of 2 cm around and inside clumps of *Allocasuarina verticillata*.

Soils. These were studied from soil pits dug at various intervals along the transects. Horizons were described and sampled for analysis of particle size distribution, ped structure, pH (1:5 soil:water), total N, HCO3- extractable P and exchangeable cations (Technicon Instruments 1977; Page et al 1972). In the winter of 1989, which in August was 46% wetter than average, the depth of the perched water table was measured in saturated heathland soils.

Vegetation

Community classification and structure. Quadrats (10 m x 2 m) were sampled every 10-20 m along each of 6 transects. The cover rating of all 113 species in 143 quadrats followed a Braun Blanquet scale (+= <1%, 1=1-5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-100%). The data set was subjected to a polythetic agglomerative classification which was truncated at the 11 group level. The groups were subsequently ordinated by non-metric multidimensional scaling. All analyses were undertaken using the PATN package (Belbin 1987).

The structure of various communities was depicted by bisect profiles. The density and height of trees and shrubs was assessed by the point-centred quarter method (Catana 1963). *Allocasuarina* clumps were analysed by a contiguous grid of 2x2 m plots in which species composition and density of stems was recorded. The litter layer of *Allocasuarina* clumps was collected from five quadrats (0.5 x 0.5 m) and compared with that from a similar number of plots under *E. obliqua* clumps and nearby heath of *L. scoparium*. The mean dry weights and concentration of total N and P were determined.

Chlorosis in Leptospermum scoparium. During the course of the vegetation survey, chlorosis in this species was observed where it was growing near many of the cliff edges. The growth, form and leaf colour of *L. scoparium* was studied in a pot experiment in the glasshouse at Melbourne University. Seed from both chlorotic and green bushes at Port Campbell were sown into plastic pots (n= 10) of marl collected from the cliff edge where chlorosis was apparent, and from top soil of heath 200 m inland, where chlorosis was absent. To test whether chlorosis could be alleviated by anoxic soil conditions, chlorotic plants, 2 months old and 10-20 cm high, were grown in drained marl then subjected to waterlogging to within 1 cm of the soil surface for several weeks. They were then reaerated for a similar period and the results qualitatively assessed. To test whether chlorosis was due to iron deficiency, six month-old, chlorotic seedlings growing on free- drained marl were treated with iron chelate (2 p.p.m. Fe EDDHA) at a rate of 190 ml-over 14 days and the results qualiatively compared with control plants.

Results

Local climate and aerial salt collection. In late summer-early autumn on sunny days with sea breezes, cliff-top air temperatures were frequently 3-4 °C lower, wind speeds and relative humidities higher than those 300-400 m inland. The concentration of Cl^- in each year of study showed the marked effect of sea breezes on aerosol salt collection. The Cl^- concentration in the salt traps as well as Na^+ concentration in the top soil was high at the cliff edge and fell sharply with increasing distance inland (Figs. 9 a,b). The Cl- concentration on the foliage of various species generally followed the trend of that recorded from the traps. However, although it was greatest on the windward sides of dense-foliaged plants, this trend was reversed in plants with sparse foliage. Salt spray tolerant species had thick cuticles or surface mats of dead hairs (e.g. *Calocephalus brownii*) which would have prevented much of the salt from reaching the living leaf tissues. In general, salt was highest on foliage near the cliff edge and on emergent vegetation.

Soils. Typical profiles of various soil types on the Tertiary deposits are shown in Fig.6. The sandy loam top soils were of variable depth (20-40 cm), usually with a pale grey A2 horizon. The amount of buckshot gravel was also variable hut often made up 10-40% by weight of the horizon sample.

During the very wet winter of 1989, holes dug in the heathland near Quarry Trail on a very gentle seaward slope showed a perched water table at depths of 0-2 cm. In places, where surface seepage occurred (Fig.10), bare soil surfaces were covered with strands of filamentous green algae oriented downslope as a result of water movement. In winter, many areas of soil in wet heath showed large patches of gelatinous blue-green alga, *Nostoc commune*, which no doubt contributed to the nitrogen status of the top soil. The structure of these soils showed less disaggregation in the top soils than sub soils. By contrast, the calcareous loam near the cliff edge was well drained and showed minimal profile development.

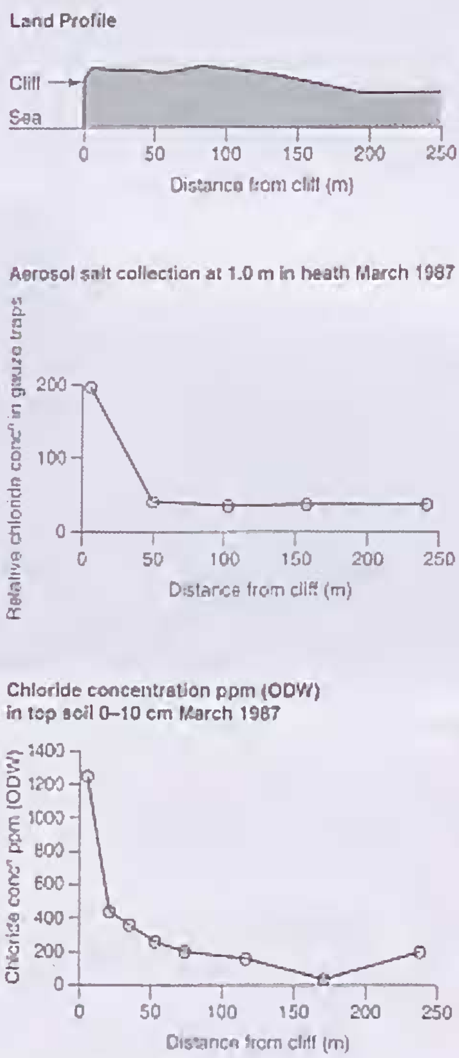


Fig. 9. A. Chloride concentration in aerosol traps at different distances from the cliff , Sentinel Rock transect, March 1987. B Chloride concentration in top soil, Sentinel Rock transect, March 1987

Depending on the particular site, the pH of top soils decreased from 7.5 - 8.5 near the cliff edge to 5.8 - 6.3 at a distanee of 300-500 m inland (Fig. 11). The trend of the pH of the sub soils was generally similar to that of the top soils. Along two transects regression analysis showed that both the pH and the total of four exehangeable eations (Na,K, Ca, and Mg) decreased signi-ficantly ($p < 0.05$) with increasing distance inland. Calcium aecounted for most of the exchangeable cations measured. At Quarry Trail the coastline is normal to the prevailing on-shore SW winds and exchangeable Ca showed a linear decline with distanee inland from the eliffs. At the Sentinel Rock transect site however, the relationship is eurvilinear, due probably to the large embayment of the eoastline to the west (Fig. 1) which allowed SW winds undue influence on a large section of the transect (Fig. 12). The average concentration of Ca^{++} in top soils was twiee that in the sub soil, whereas that for Mg^{++} this ratio was only about one third. Exehangeable Na^{+} and K^{+} as well as extraetable Cl^{-} in both top soil and subsoil was higher near the cliff than inland. As expected, total nitrogen values paralleled those of organie earbon and were thus greater in top soil than sub soil and considerably greater under dense clumps of *Allocasuarina verticillata* than in adjacent heathland. Bicarbonate-extractable P in top soils was generally low and varied from 10 to 15 mg/kg and showed no trend over a distanee of 420 m from the cliff.

Fig. 10. Seepage of perched water table from the soil surface, Quarry Trail July 1989

Plant Communities

Their composition, structure and zonation. The classification (not depicted) was truncated at the 11 group level, but was interpreted for the purposes of the ordination, at the five group level, A-E (Fig. 13). The species frequency of species arranged in these groups suggests a continuum (Table 1). The broadest groupings viz. A, B+C and D+E correspond approximately to the zonation described by Grant (1987). The zones varied considerably in width from one transect to another and not all groups were present in every transect. Axis 1 appears to be related to factors concerned with distance from the cliffs. Groups B and C appear to seggregate along Axis 2 which may be related to distance along the coastline. Groups D and E occur in the same zone and may be discriminated by local habitat factors which may be resolved by additional quadrats. Although there is a high degree of floristic similarity between groups B and C as well as between groups D and E there are sufficiently important differences in the frequencies of dominants and sub-dominants of shrub, forb and graminoid strata to suggest that they remain distinct

Profiles of the main communities are shown in Fig. 14. On many of the stripped cliff edges, such as those at Loch Ard, Broken Head and Quarry Trail, very open halophyte communities contain *Sarcocornia blackiana*, *Samolus repens*, *Selliera radicans* and *Wilsonia humilis* and *W. backhousei*. (Fig 14a). Where the original soil mantle persisted, the community present (Group A) was an open grassy heathland (Fig. 14 b) of *Poa poiformis* and cushion bush (*Calocephalus brownii*). This was similar to that recognized by Grant (1987), but it also contained *Olearia axillaris*, *Lepidosperma gladiatum*, *Tetragonia implexicoma* and *Samolus repens*. Further back on marl, up to 50-100 m from the cliff, the community (Group B) was a grassy heathland dominated by *Leucopogon parviflorus* and *Poa poiformis* with *Olearia axillaris*, *Acrotriche prostrata* and numerous forbs (Fig. 14c). Further inland, 100-200 m inland from the cliffs, the community (Group C) was heathland dominated by *Leptospermum scoparium* and *Hibbertia aspera* (Fig. 14d). Beyond this distance, 200-300 m inland, the community (Group D) was dominated by *Leptospermum scoparium* and *L. continentale* (Fig. 14 e,f). Groups A-D were distinguished by a change in the graminoid components: thus grasses were dominant in A and B whilst sedges (*Gahnia trifida* and

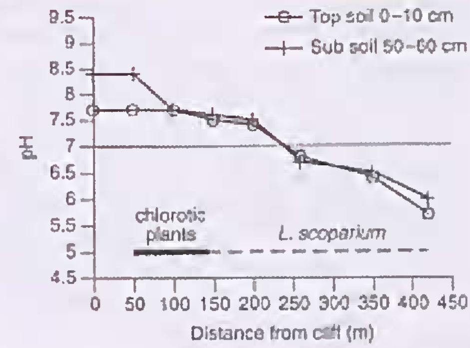


Fig. 11. pH in top soil and subsoil at different distances from the cliff at Quarry Trail.

Schoenus nitens) and rope rushes (*Baumea juncea*) were conspicuous in C and D. Furthest inland at 400-500 m, the community (Group E) was a low open woodland or forest 3-10 m tall, dominated by *E. obliqua* and *E. ovata* (Fig. 14 g). The understorey was heathy, and rich in those sclerophyll species, such as *Isopogon ceratophyllus*, *Allocasuarina paludosa* and *Xanthorrhoea australis*, that are typical of many other heathlands in southern Victoria.

Under the denser clumps of eucalypts, tangles of *Hibbertia aspera* were common and ground stratum species were suppressed. The humus horizon in such sites was commonly matted into a compact layer up to 10 cm thick, resembling fibrous mor in dry sclerophyll forests of southern Tasmania and parts of Wilsons Promontory.

In some heathlands within 200 m of the cliff,

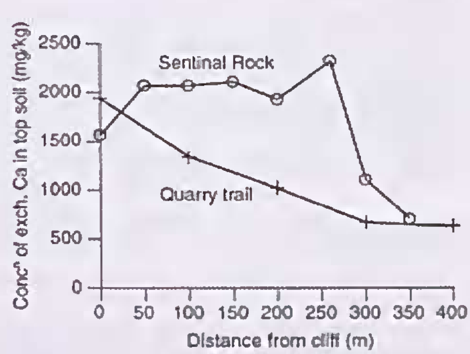


Fig. 12. Concentration of exchangeable calcium in top soil with increasing distances from the cliffs, Sentinel Rock and Quarry Trail.

Species Groups	A (n=9)	B (n=39)	C (n=65)	D (n=23)	E (n=7)
Shrubs-Trees:					
Calocephalus brownii	44 (33)	35 (17)	11 (6)	· ·	· ·
Olearia axillaris	44 (11)	35 (17)	48 (15)	· ·	· ·
Tetragonia implexicoma	33 (33)	22 ·	5 ·	· ·	· ·
Ozothamnus turbinatus	· ·	17 ·	2 ·	· ·	· ·
Leucopagon parviflorus	· ·	43 (9)	85 (53)	23 ·	43 ·
Leptospermum scoparium	· ·	48 (39)	58 (49)	100 (97)	100 (86)
L. continentale	· ·	35 (26)	2 ·	54 (31)	14 (14)
Bossiaea prostrata	· ·	13 ·	2 ·	33 ·	· ·
Hibbertia aspera	· ·	· ·	51 (34)	51 (44)	57 (57)
Banksia marginata	· ·	· ·	18 ·	49 ·	29 (14)
Astrolama humifusum	· ·	· ·	14 ·	38 (3)	14 ·
Acrotriche prastrata	· ·	· ·	37 (20)	8 ·	· ·
A. serrulata	· ·	· ·	· ·	23 ·	· ·
Eucalyptus obliqua	· ·	· ·	· ·	10 (8)	71 (57)
No. spp.	3	8	12	10	7
Graminoids:					
Poa poiformis	100 (55)	96 (78)	82 (60)	10 ·	43 ·
Tetrarrhena distichophylla	· ·	61 (22)	3 ·	31 ·	43 ·
Baumea juncea	33 (11)	4 ·	60 (15)	61 (36)	14 ·
Gahnia trifida	· ·	74 (22)	74 (58)	66 (51)	· ·
Schoenus nitens	· ·	48 (13)	65 (8)	64 (18)	14 ·
Carex breviculmis	· ·	4 ·	29 ·	56 ·	29 ·
Isolepis nodosa	· ·	48 ·	3 (2)	· ·	· ·
Themeda triandra	· ·	· ·	5 ·	18 ·	43 (29)
Lepidosperma filiformis	· ·	3 (2)	13 ·	· ·	· ·
Danthonia spp. (3)	· ·	· ·	33 (4)	10 ·	· ·
No. spp.	2	8	13	11	6
Forbs:					
Sarcocornia blackiana	55 ·	· ·	· ·	· ·	· ·
Samolus repens	55 ·	48 ·	42 ·	5 ·	· ·
Selliera radicans	22 ·	35 ·	78 (21)	28 ·	14 ·
Senecio lautus	55 ·	43 ·	12 ·	· ·	29 ·
Apium prostratum	55 ·	4 ·	11 (3)	· ·	· ·
Lobelia alata	22 ·	· ·	29 ·	3 ·	14 ·
Oxalis 'corniculatus'	11 ·	70 ·	20 ·	10 ·	14 ·
Leontodon taraxacoides	11 ·	17 ·	52 ·	20 ·	43 ·
Brachyscome parvula	11 ·	· ·	60 ·	5 ·	· ·
*Centaurium erythraea**	· ·	48 ·	77 ·	77 ·	14 ·
Dichondra repens	· ·	· ·	29 ·	18 ·	29 ·
No. spp.	9	7	10	8	7
Total number of spp.	14	23	35	29	20

Percent frequency of species in quadrat groups A-E zoned from the cliff inland for 300-400m. ( )=% Frequency of cover values ³ 5%. n = number of quadrats. * introduced.

Table 1. Species composition of vegetation groups

small areas of bare soil 50-100 cm in diameter may be partly vegetated by short turfs of *Schoenus apogon* and occasional prostrate halophytes, such as *Samolus repens* and *Selliera radicans*.

The dominant shrubs in Groups A-D varied in density with proximity to the cliff (Fig. 15). Vegetation decreased in height closer to the cliff edge where salt wind was strongest. In the cliff-top zone species were differentiated according to their tolerance to aerial salt. Thus, *Leucopogon parviflorus* and *Olearia axillaris* and the upper dead foliage of grasses and sedges overtop and partly protect low shrubs of *Hibbertia aspera* and *Leptospermum scoparium*. Dwarfed eucalypts in zones near the clÃiffs were pruned to the height of the heath but further back they formed emergent streamlined clumps or low forest. Emergent clumps of *Allocasuarina verticillata* were distinctly different.

Status of clumps of emergent Allocasuarina verticillata *and* E. obliqua. In each of Groups B to E, *A.verticillata* occured as dense, isolated clumps 5-25 m in diameter, and consisting of 100 or more stems 4-8 m tall. They occurred from the cliff edge sporadically through much of the heath zone and low eucalypt forest. *A. verticillata* also occurred in taller groves on shallow limestone soil on the sides of the Port Campbell creek valley, 1-2 km inland. Clumps of *A. verticillata* in the heath may be even aged with a compact profile or uneven aged with an uneven profile. Although *A. verticillata* is salt-wind resistant, it tended to lean away from the coast and, in the most exposed

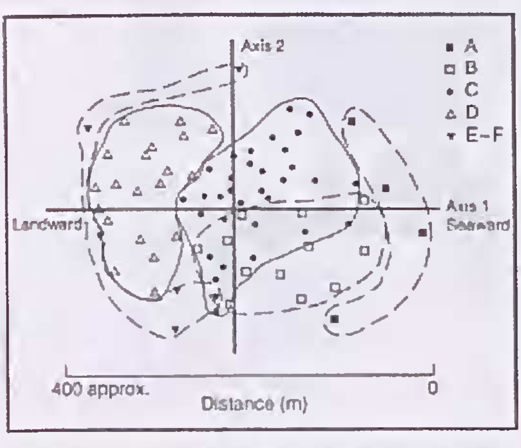


Fig. 13. Ordination of 5 major quadrat groups. Axis 1 correlates with distance from the cliff edge.

sites died back on the seaward side. Stress-affected plants commonly showed damage from wood boring larvae. Even-aged clumps (Fig. 16) were likely to have originated from past fires since charred remains of original stems were invariably present in the interior of the clumps. In uneven-aged clumps (Figs. 17, 18) a preponderance of dead and dying stems occurred in the centre of the stand and younger individuals occurred at the periphery. It appears that such clumps had not been burnt for a considerable time. *A. verticillata* regenerated principally by suckering from shallow roots at depth between 0.5 and 2.0 cm. and especially where the surrounding heath was low and bare soil exposed. Heath on the seaward side of clumps tended to be shorter than that flourishing in the wind shadow. The surface soil temperature on a warm autumn day was 3-4°C higher in the low heath on the immediate windward side than in the taller heath on the leeward sides of clumps (Table 2). This may be a reason for the stimulation of shoot development from shallow lateral roots on the seaward side of clumps. This type of regeneration has resulted in the clumps gradually extending seaward.

The taller, more salt-wind resistant *A. verticillata* may protect non-resistant species. Thus at Two Mile Bay, exposed *E. ovata* is wind pruned to the level of the heath (1 m) except in the immediate lee of *A. verticillata* when it equals the height of the protecting species (7 m).

The clumps tend to be dioecious, and about two thirds were male. No fruits were found in any female clumps exposed to onshore winds, although 300-400 m inland occasional fruits occurred on the lee side of the clumps. By contrast, along the valley of the Port Campbell creek 1 km inland, female trees are laden with fruits. The percentage of viable seed from cones in inland stands was 38% compared to 1.2% in heathand clumps. Mean seed weight from trees on the exposed sites was only 40 % of that on trees in protected sites. Associated species in the clumps were few -eg. *Rhagodia candolleana*, possibly due to low light intensity, root competition and a very thick, loose litter layer up to 20-50 cm deep.

The weight of loose litter on the floor of clumps of *A. verticillata* was 5.22± 3.45 kg m^{-2} or 9.7 times greater than that in adjacent *L. scoparium* heathland and 17.4 times greater than under clumps of dense *E. obliqua* (Table 2). Slow decay of the fibrous litter may be one of the reasons for the large differences in accumulation of material on the soil surface. The light intensity in *A. verticillata* clumps is considerably greater than

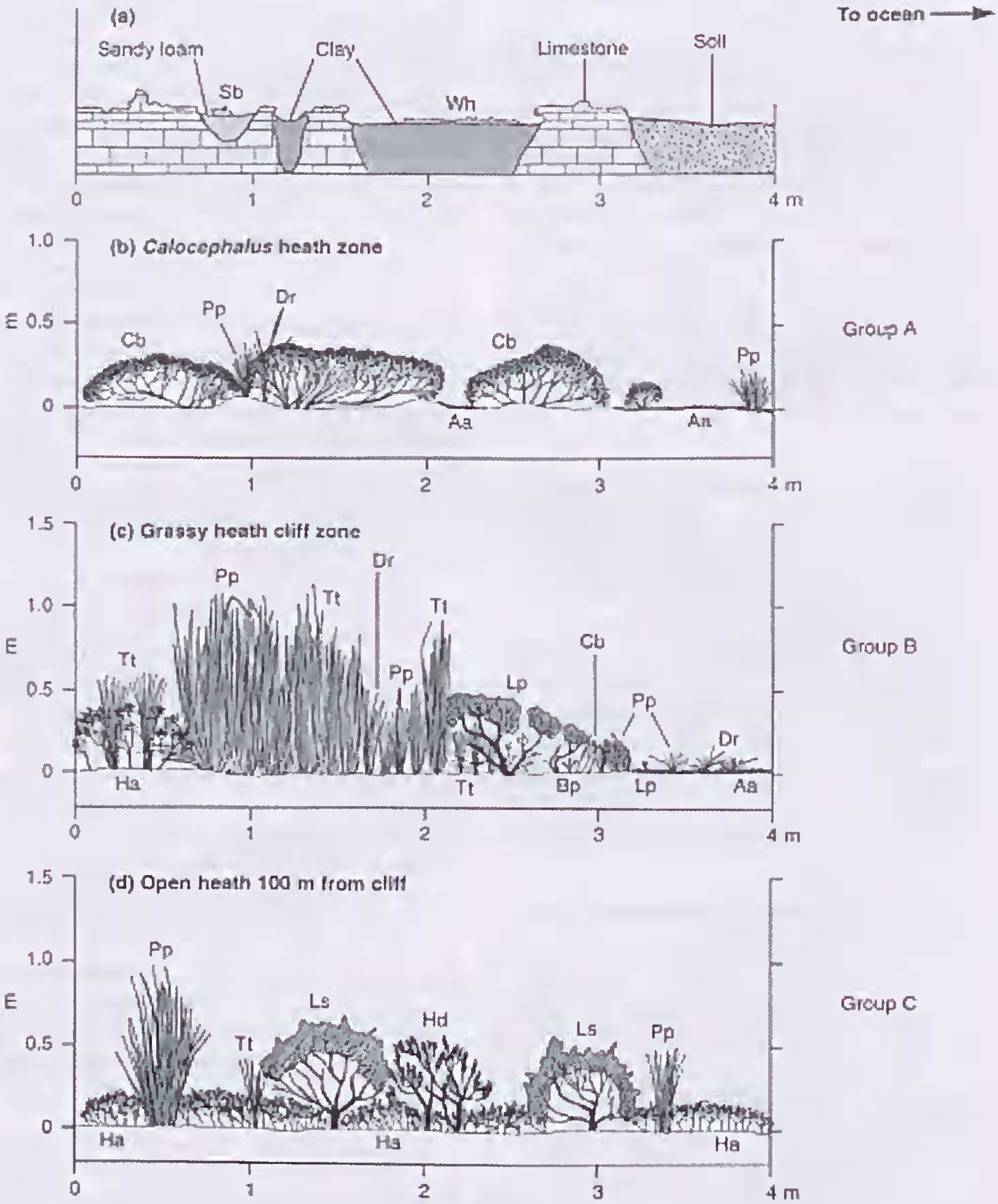
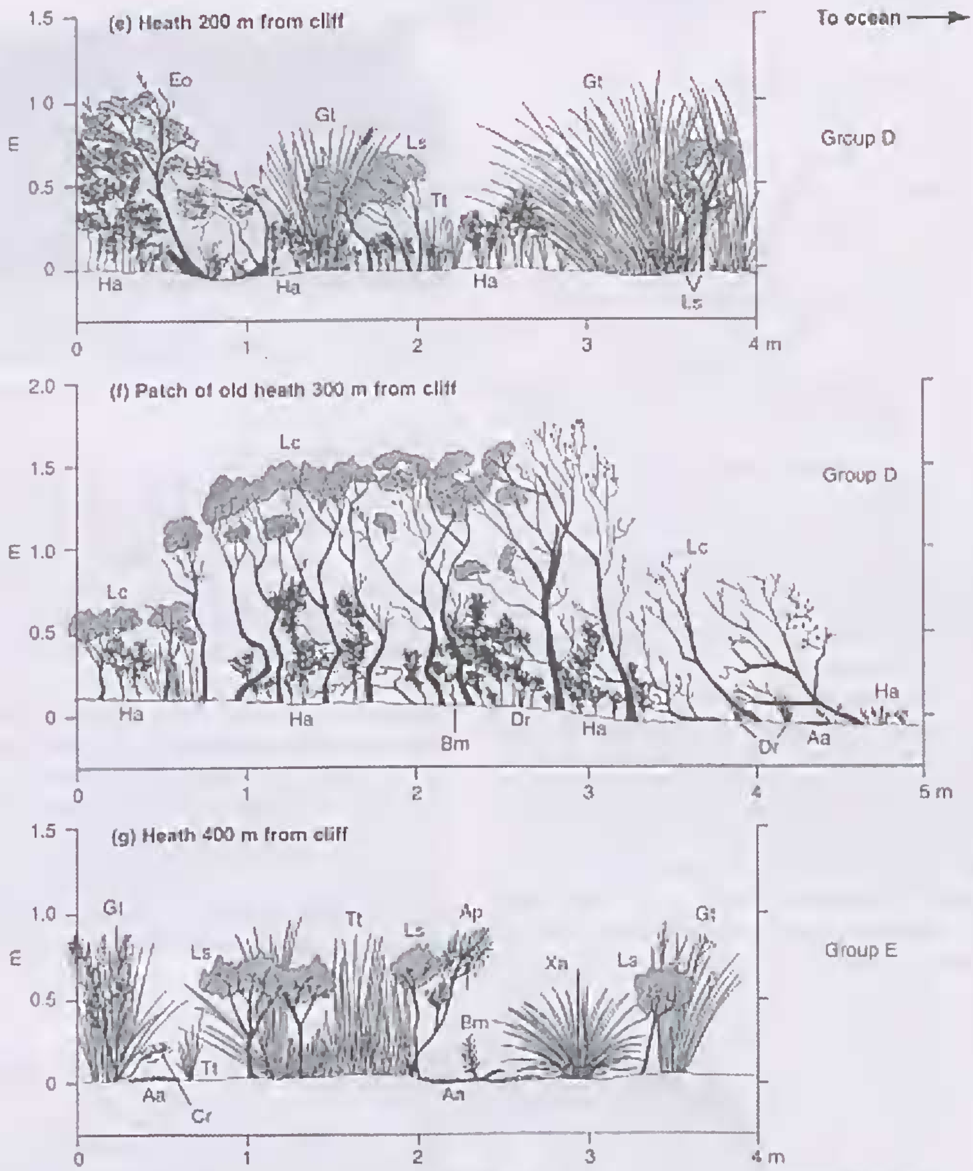


Fig. 14. (a)-(g). Profiles of various communities which conform to quadrat groupings A,B,C,D and E.



Key:

Aa	*Acrotriche affinis*	Eo	*Eucalyptus obliqua*	Pp	*Poa poiformis*
Ap	*Allocasuarina paludosa*	Gt	*Gahnia trifida*	Sb	*Sarcocornia blackiana*
Bm	*Banksia marginata*	Hd	*Helichrysum dendroideum*	Tt	*Themeda triandra*
Bp	*Brachyscome parvula*	Ha	*Hibbertia aspera*	Wh	*Wilsonia humilis*
Cb	*Calocephalus brownii*	Lc	*Leptospermum continentale*	Xa	*Xanthorrhoea australis*
Cr	*Correa reflexa*	Ls	*Leptospermum scoparium*		
Dr	*Dianella revoluta*	Lp	*Leucopogon parviflorus*		

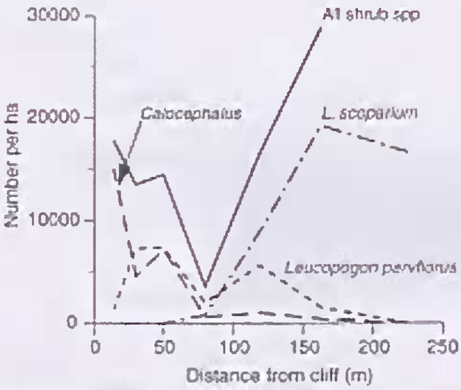


Fig. 15. Changes in density of major dominant shrubs with increasing distance from the cliff, Loch Ard area.

Fig. 16. Photograph of dense, emergent even-aged clump of *Allocasuarina verticillata*, Sentinel Rock.

under dense *E.obliqua* (Table 2). The number of associated understorey species is lower under *E. obliqua* than *A. verticillata*, although the effect of the cover of the latter species was only apparent when its cover exceeded 50-75%. The levels of N and P in the litter layer suggests that dense clumps of *C. verticillata* act as 'islands' of comparatively high nutrient accumulation in this heathland.

E. obliqua occasionally occurred as a wind-pruned component of the heath stratum (Fig. 14e) and became a wind-smoothed emergent beyond 250 m from the coast. Emergent clumps of *E. obliqua*, consisting of 10 or more trees form an aggregate smoothed profile 4-5 m high in the heath about 400 m from the cliff (Fig. 19) and with increasing distance are taller and coalesce to form low, dry sclerophyll forest. Eucalypt regeneration is very rare and probably restricted to post-fire periods.

Fire in heathland

Most of the heathland area shows at least some evidence of past fire.In the heathlands opposite Sentinel Rock, small patches of long unburnt *L. scoparium* and *Hibbertia aspera* heath were taller and denser than surrounding heath and less species-rich.

Where *Banksia marginata* occurred it was possible to provisionally age the vegetation since this species produces two nodes in the first year after a fire and one per year thereafter. Most of the heathland studied was at least 12-15 years old whilst the taller heath patches appeared to be about twice that age. A small fire of about 0.1 ha, in heathland dominated by *Leptospermum scoparium* and *L. continentale* occurred in March, 1987. This killed all above-ground parts but within a few weeks the fire resistant species had begun to resprout from lignotubers and under-

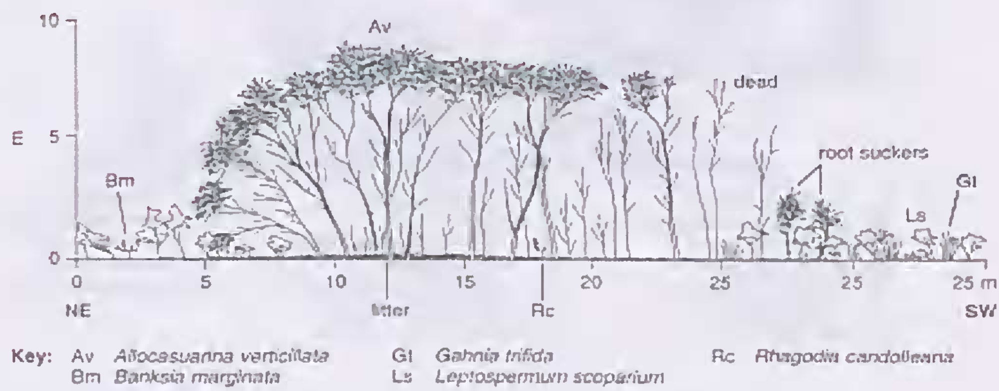


Fig. 17. Profile of uneven-aged clump of *A verticillata*, Sherbrooke River.

	Leptospermum spp. heath	*Allocasuarina verticillata*	*Eucalyptus obliqua*
Environment:			
Max. air temperature in March22.4°C			
Soil temp. 0-2 cm at midday, March	Seaward of *Allocasuarina* 27.2°C Landward of *Allocasuarina* 14.2°C	14.2°C	
Light intensity at 0.5 m			
Diffuse light (% sky)	62.8%	24.6%	17.8%
Direct light (% suntrack)	39.7%	15.5%	6.3%
(Mean of solstices & equinoxes)			
Litter floor			
Total d.wt. kg/m² ± SD	0.68 ± 0.28	5.22 ± 3.45	0.30 ± 0.04
N content g/m²	36.83	479.65	17.66
P content g/m²	1.23	8.66	0.77

Table 2. Environment and litter floor characteristics in *A verticillata* and *E. obliqua* clumps compared with adjacent mainly *L. scoparium* heath.

ground parts. Seedlings appeared in late autumn and in the following spring. The most important finding was that *L. scoparium* was not lignotuberous and not fire resistant (Fig. 20) and regenerated only from seed, whilst *L. continentale* (Fig. 21) and *Allocasuarina paludosa* regenerated vigorously from lignotubers as well as from seed. *Leucopogon parviflorus* sprouted from the lower stem and also regenerated from seed, whereas *Banksia marginata* sprouted mainly from shallow lateral roots.

Soil-plant interaction

Chlorosis in Leptospermum scoparium. Towards the cliff edge this shrub decreased in height and suffered severe pruning from salt wind. At about 20 m from the cliff edge it was prostrate, although protected to some extent by taller and more resistant species such as *Hibbertia aspera.* Where it encroached onto the calcareous marl deposits in this zone it was conspicuously yellow, particularly on the sunnier sides of the bush. The zone of chlorosis coincided with the zone of friable calcareous marl, indicating that this species is a calcifuge. Glasshouse experiments demonstrated that within a few weeks, chlorosis occurred only in seedlings raised in the calcareous top soils from near the cliff edge, irrespective of the seed source. Chlorosis was therefore not genetically based but environmentally determined. Morphological differences were also clear cut: chlorotic plants were very bushy and stunted, whilst normal plants at this stage under these conditions were tall with few axillary branches (Fig.22). The addition of iron chelate (Fe EDDHA) to seedlings over several weeks only partially removed chlorosis, however when chlorotic plants in calcareous soil were waterlogged they all rapidly turned green. This effect was rapidly reversed if such soil was allowed to aerate.

DISCUSSION

Vegetation Zonation

On-shore coastal winds laden with salt spray are probably the most important factors shaping the form and composition of plant communities in coastal environments. Communities are zoned parallel to the coast

Fig. 18. Photograph of a degenerate clump of *A.verticillata* near the cliff, Sentinel Rock, showing copious regeneration from root suckers.

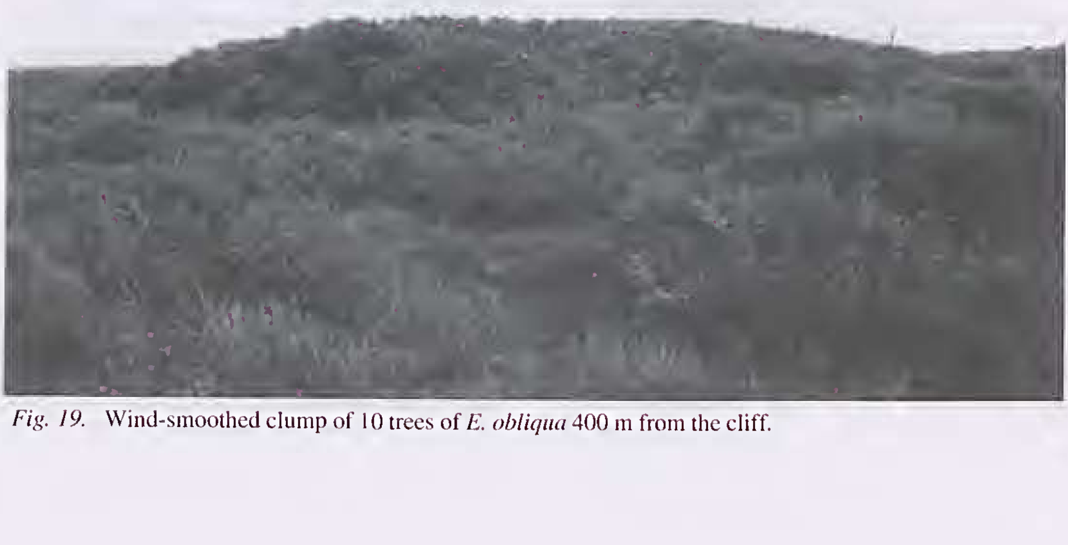


Fig. 19. Wind-smoothed clump of 10 trees of *E. obliqua* 400 m from the cliff.

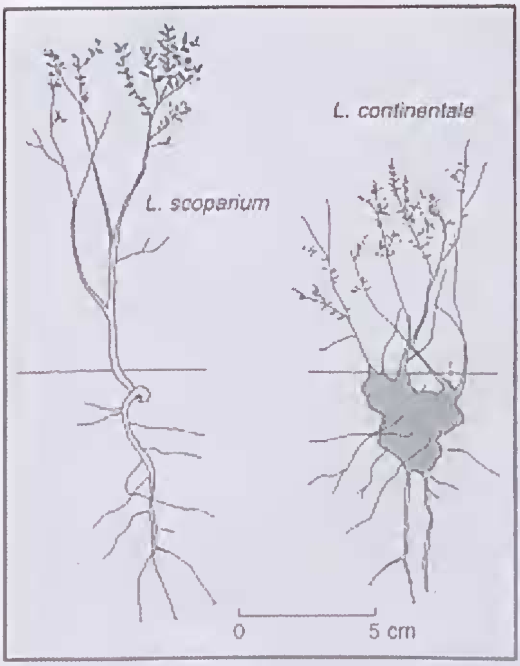


Fig. 20. Drawings of young *L .scoparium* and *L. continentale* showing absence and presence of lignotuber development

and any relief from such wind results in an increase in canopy height and a change in species composition, either from the reduction of saline aerosols *per se* or from the competition imposed by taller species. At Port Campbell, the zonation of vegetation ranges from short, grassy open heathland close to the cliffs to closed sedgey heathlands and woodlands further inland. The most rapid changes occur in the first 10-30 m from the cliff edge for it is here that winds are strongest and the concentration of deposited salt greatest. In general, the distance of species from the cliff edge is related to their relative resistance of aerial salt.

Salt intolerant species are severely wind-pruned where they extend above streamlined canopy profiles (Boyce 1954, Parsons and Gill 1968). However Parsons (1981) has pointed out that input of the major cations (K, Na, Ca, Mg) derived from rain is at least 50% of that recorded as 'dry fall out' and that the

Fig. 20. Recovery of heath in August 1989 following fire in March 1987 along Quarry Trail. Shrub on left is *Leucopogon parviflorus* coppicing from the base, shrub on the right is *Leptospermum scoparium* which has been completely killed.

Fig. 22. Seedlings of *L. scoparium* (left) grown in drained marl soil (bushy chlorotic plant) and podzolic top soil (tall, unbranched non-chlorotic plant). Subsequent waterlogging of such plants after pots were encased in plastic bags (right), resulted in the full greening of plant in marl soil

canopy impaction of such elements may be 2.3-3.0 times higher. Boyce (1954) pointed out that in salt spray communities in North America, where there are strong onshore winds the whole of the foliage may intercept aerial salt. In many of the cliffs exposed to the strongest wave action, large storm waves splash onto the cliff top creating soil salinity and contributing to erosion of soil and limestone. The thin soils on these harsh sites are colonized by low halophytic plants forming very open communities.

The heathland along the Port Campbell clifftops is unusual due to the occasional presence of small, scattered halophytes such as *Selliera radicans* and *Samolus repens*. They occur on flat terrain associated with low swards of *Schoenus apogon* in small, slightly depressed gaps, 0.5-1.0 m in diameter, and are likely to indicate local accretion of cyclic salt, at least in some years.

One important feature of the cliff top vegetation at Port Campbell is the influence exerted by the limestone cliffs on the surface soil. Since calcilutite is relatively soft it is susceptable to considerable wind and water erosion. Dislodged heavier material is deposited close to the cliff edge whilst the finer material appears to be blown inland over some hundreds of metres. The calcareous marl deposit is well drained hence calcifuge species, such as *Leptospermum* *scoparium*, which encroach onto it, exhibit marked chlorosis. On this soil it is stunted and bushy, a feature which may be an advantage in a severe salt-wind environment. This species is also relatively tolerant of seasonal waterlogging and where this occurs, chlorosis is absent even though pH is relatively high. This suggests that anoxic conditions have led to the reduction of iron and an increase in its availability. The differences in soil pH between chlorotic and non chlorotic areas near Sentinel Rock may only differ by 0.5 units. Anderson & Ladiges (1978) however have shown at Cape Otway that relatively small differences in pH can be important in the development of chlorosis in *Eucalyptus* species on aeolianites.

Although Na+ from salt aerosols also decreases from the coast and may affect soil pH), exchangeable Ca is present in far greater amounts. It seems likely that much of the pH gradient across the heath is due to fine calcareous material carried from the cliff face by on-shore winds. Concentrations of exchangeable cations in the topsoil are greater than in the subsoil, a feature which could be explained by such aerial accretion or by nutrient enrichment derived from litter decomposition. The generally low P concentration in the soil is consistent with the general work of Specht (1979). Soils on the lateritized Pliocene sediments are markedly duplex and leached and are similar to soils of other ground water heaths in Victoria (Groves & Specht 1965). However, they differ from other coastal heath sites by their neutral to moderately acid pH. Intermittent perched water tables in such soils, which are indicated by the prevalence of buckshot gravel, create considerable stress to plants because of anoxicity, relatively impeded root systems and the subsequent occurrence of summer droughts (Groves and Specht 1965; Specht 1981). The presence of *Gahnia trifida* and *E. ovata* in the heath is often indicative of seasonal waterlogging, at least in the sub-soil.

Allocasuarina verticillata is a widespread small tree growing over a wide range of mostly dry habitats. Its conspicuous emergence in the Port Campbell heathland testifies to its extreme resistance to salt wind which to some extent, may be related to the tendency of its strongly xeromorphic foliage to 'flow in the wind'. *A. verticillata* is wind pollinated and the extreme paucity of fruiting in female plants on the exposed heathlands could be due to damage inflicted on the exposed, feathery stigmas by salt winds. The origin of the emergent clumps is somewhat enigmatic since they are clonal, propogate peripherally by root suckering and produce very little, if any seed. It seems likely that winged seed has been blown onto the heathland from fertile stands 1-2 km inland inland, probably as a result of a past fires associated with hot northerly winds. After fire, dense, vegetative regeneration of this species produces even-aged patches. Long unburnt clumps on the other hand, are uneven-aged. The litter layer is extraordinarily deep (20-50 cm), slow to decay and therefore represents considerable local accumulations of nutrients, such as N.

Most of the heathland area shows at least some evidence of past fire. From the morphology of associated *Banksia marginata* it was possible to provisionally age the vegetation, most of which was was at least 12-15 years old. A small fire in 1987 revealed that most heathland species recovered vegetatively by way of lignotubers, coppice, root suckers and rhizomes as well as by seedlings. Such observations were consistent with those of many others workers (Russell & Parsons 1978, Specht 1979, and Wark 1996). The most important finding was that *L. scoparium* was in this area is not fire resistant but regenerated copiously from seed after fire. Seedlings in unburnt heath are extremely rare. Preliminary observations suggest that the initial non-flowering period may be 4-5 years, hence if these heathlands had been burnt very frequently in the past, this species would have been eliminated.

Species richness (number per quadrat) across the heathland area varied between communities. It was least both at the cliff edge and inland under dense wind-pruned *E. obliqua* clumps. It reached a maximum in mixed heath on acid soils 200-300 m inland, but was markedly reduced in old patches of taller heath dominated by *Leptospermum scoparium* and *Hibbertia aspera*. Such reduction of species richness with age of heath is consistent with work on the Dark Island heaths of South Australia by Specht et. al.(1958) and ground water heaths of Wilsons Promontory by Russell & Parsons (1978). Fire within a particular frequency range is necessary to restore the biodiversity of heathlands dominated by obligate seeders and, to this extent the ecology of *L. scoparium* at Port Campbell is somewhat analogous to that of *Banksia ornata* in the drier heaths of Victoria and South Australia (Gill & McMahon. 1986).

ACKNOWLEDGEMENTS

We wish to thank The Department of Conservation and Environment for permission to work in this area. Much information in the earlier years was collected with the help of senior ecology students and numerous colleagues. We are indebted to Dr. E. Bird and Dr. R.F. Parsons for commenting on the manuscript and to Dr. Bird for his insights into geomorphological processes.

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Manuscript received 12 January 2001
Revision accepted 9 March 2002